Larval development of five species of blenny (Teleostei: Blenniidae) from the western central North Atlantic, with a synopsis of blennioid family characters

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Light trap collections on oil and gas platforms in the northern Gulf of Mexico off Louisiana from 1995 to 1997 contained young of tessellated blenny *Hypsoblennius invemar*, freckled blenny *Hypsoblennius ionthas*, featherduster blenny *Hypleurochilus multifilis*, molly miller *Scartella cristata* and seaweed blenny *Parablennius marmoreus*, which are described. Interspecific differences were: number of dorsal, anal, pelvic and caudal fin elements; number of mandibular pores; presence or absence of canine teeth, hypural 5 and pectoral fin pigment; width of gill openings; length of preopercular spines (in larvae). Size at settlement differed among some taxa, but all five species settled within a narrow size window of *c.* 1·5 mm standard length (L_S). *Hypsoblennius invemar*, *H. ionthas*, *H. multifilis* and *S. cristata* settled at mean sizes between 11·3 and 12·1 mm L_S, whereas *P. marmoreus* settled at a mean size of 19·3 mm L_S. Sexually dimorphic differences were consistently evident by 17–18 mm L_S in all species but *P. marmoreus*. The two smallest blennies with external characters normally associated with sexual maturity were a 20 mm male and 21 mm female *H. multifilis*. Primary caudal fin rays began to bifurcate between 17·0 and 18·3 mm L_S in *H. invemar*, *H. ionthas*, *H. multifilis* and *S. cristata*. *Hypleurochilus multifilis* displayed the external characteristics of being sexually mature at 20–21 mm L_S. Thus, bifurcation of primary caudal fin rays was an indicator of approaching sexual maturity in *H. multifilis* and this may also be true in the other species studied. © 2005 The Fisheries Society of the British Isles (No claim to original US government works)

Key words: dimorphism; intervals; metamorphosis; meristics; sexual maturity.

INTRODUCTION

The taxonomically and ecologically diverse group of marine fishes known as blennies (Teleostei: Blenniidae) includes nine genera and 20 described species from the western central North Atlantic area (WCNA; Table I). Blenniids are small, scaleless, sexually dimorphic fishes with jugular pelvic fins of two to four soft rays each. They are demersal or semi-demersal and generally reside in reef or 'biofouling'

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TABLE I. Meristic and other data for members of the family Blenniidae from the western central North Atlantic area. Genetic evidence suggests two distinct lineages of *Ophioblennius* in the area covered (Muss *et al.*, 2001). All species have a mode of 13 segmented primary caudal fin rays, except *Chasmodes* (11–12). Only *Scartella* has the lower pectoral fin rays thickened

Taxa	Dorsal spines + soft rays (mode)	Total dorsal elements (mode)	Total anal elements (mode)	Total vertebrae (mode)	Pelvic rays (mode)	Pectoral rays (mode)	Caudal rays, upper + primary + lower = mode total elements	Epurals
Chasmodes								
bosquianus	X–XI (XI) + 16–19 (18)	28–30 (29)	18–22 (20)	34–35	I, 3	11–13 (12)	4 + 11 – 12 + 3 – 4 = 19	1
saburrae	X–XIII (XI) + 16–20 (18)	27–31 (28–30)	19–21 (20)	34–36 (34)	I, 3	11–13 (12)	4 + 11 – 12 + 3 – 4 = 19	1
Entomacrodus								
nigricans	XII–XIII + 13–16 (14–15)	(27–28)	16–19 (18)	33–35 (34)	I, 4	13–14	N/A	1
vomerinus	XII–XIV (XIII) + 15–17 (16)	28–30 (29)	17–20 (19)	34–36 (35)	I, 4	12–15 (14)	N/A	1
Hypleurochilus								
bermudensis	XI–XII (XII) + 12–13 (13)	25	16–17 (17)	30–31 (31)	I, 4	13–14 (14)	N/A	1
caudovittatus	XII + 14–15 (14)	26–27 (26)	17–19 (18)	33	I, 3	14	5 – 6 + 13 + 4 – 5 = 23	1
geminatus	XII + 14–16 (15)	26–28 (27)	16–20 (18–19)	32–33 (33)	I, 3–4 (3)	13–15 (14)	5 – 6 + 13 + 4 – 5 = 23	1
multifilis	XII + 13–16 (15)	26–27 (27)	17–20 (18–19)	32–33	I, 3	14	5 – 6 + 13 + 4 – 5 = 23–24	1
pseudoaequipinnus	XI–XII (XII) + 11–15 (13–14)	25–26	16–18 (17–18)	31–32 (32)	I, 3–4 (4)	13–15 (14)	4 – 6 + 13 + 4 – 5 = 22 – 24	1
springeri	XI–XIII (XII) + 12–13 (13)	25	16–18 (16–17)	32	I, 4	13–15 (14)	N/A	1
Hypsoblennius								
exstochilus	XI–XII (XII) + 13–15 (14)	25–26 (26)	17–18 (18)	32–33	I, 3	13–15 (14)	6 – 7 + 13 + 5 – 6 = 25	1
hentz	XI–XIII (XII) + 13–16 (14–15)	25–28 (26–27)	16–19 (18)	31–34 (32)	I, 3	13–15 (14)	5 – 6 + 13 + 5 – 6 = 23 – 24	1
invemar	XI–XII (XII) + 11–12 (12)	23–24 (24)	15–16 (16)	30–32 (31)	I, 4	13–15 (14)	6 – 7 + 13 + 6 – 7 = 26	1
ionthas	XI–XIII (XII) + 13–15 (14)	25–27 (26–27)	16–19 (17–18)	30–33 (31–32)	I, 3	13–15 (14)	5 – 6 + 13 + 4 – 6 = 23	1
Lupinoblennius								
dispar = vinctus	XII + 13–14	25–26	17–18	31–32	I, 4	12–14 (13)	5 + 13 + 4 – 5 = 22 – 23	1
nicholsi	XII–XIII (XII) + 13–15 (15)	26–27	18–19	32–35 (33)	I, 3	13–14 (13)	5 + 13 + 4 – 5 = 22 – 23	1
Omobranchus								
punctatus	XI–XIII (XII) + 19–22 (21)	31–34 (32)	23–26 (25–26)	38–40 (39)	I, 2	12–14 (13)	6 – 8 + 13 + 6 – 8 = 25 – 29	1
Ophioblennius								
atlanticus	XII + 20–23	33–35 (33–34)	24–25	36	I, 4	14–16	N/A	2
macclurei	XII + 20–21	31–32	22–23	N/A	I, 4	14–16 (15)	7 – 8 + 13 + 7 – 8 = 28	2
Parablennius								
marmoreus	XI–XII (XII) + 17–18 (18)	30	21–22	36	I, 3	14	6 + 13 + 6 = 25	1
Scartella								
cristata	XI–XII (XII) + 14–15	26–27	17–19 (18)	33	I, 3	14	6 – 7 + 13 + 5 – 6 = 25	2

Taxa	Hypural 5	Gill opening of genus	Canines Upper	Canines Lower	Median supra-temporal pore	Last anal ray free	Dentary pores	Distribution	Primary reference
Chasmodes	(Fused)	Greatly							
bosquianus	1–0	restricted	No	No	No	Yes	4	U. S. Atlantic to northern Gulf	Springer (1959)
saburrae	1–0		No	No	No	Yes	>6	Atlantic and Gulf coasts of Florida	Bath (1977)
Entomacrodus		Unrestricted							Springer (1967)
nigricans	1		No	Yes	Yes	No	N/A	Florida, Bermuda, Caribbean	
vomerinus	1		No	Yes	Yes	No	N/A	Brazil	
Hypleurochilus		Slightly							Bath (1994)
bermudensis	1	restricted	Yes	Yes	Yes	No	4 (3 rare)	Bermuda	
caudovittatus	1		Yes	Yes	Yes	No	5	Gulf coast of Florida	Randall (1966)
geminatus	1		Yes	Yes	Yes	No	5	U. S. Atlantic coast	
multifilis	1		Yes	Yes	Yes	No	5	Northern Gulf	
pseudoaequipinnus	1		Yes	Yes	Yes	No	5	Atlantic coast of Florida, Caribbean and Brazil	
springeri	1		Yes	Yes	Yes	No	5	West Indies	
Hypsoblennius		Restricted							Smith-Vaniz (1980)
exstochilus	0		No	No	Yes	No	3	Bahamas and Virgin Islands	
henzt	0		No	No	Yes	No	4	U. S. Atlantic and Gulf coasts, but not into Mexico	
invemar	0		No	No	Yes	No	3	Gulf coast, Caribbean, Colombia, Venezuela	
ionthus	0		No	No	Yes	No	3	U. S. Atlantic and Gulf coasts	
Lupinoblennius		Slightly							Dawson (1970)
dispar = vinctus	0	restricted	Male	Both	Yes	No	3	Mexico, Central America and Caribbean	Tavolga (1954)
nicholsi	0		Male	Both	Yes	No	3	Florida	Bath (1996)
Omobranchus		Greatly							
punctatus	0	restricted	Yes	Yes	Yes	No	N/A	Caribbean	Springer & Gomon (1975)
Ophioblennius		Unrestricted							
atlanticus	1		No	Yes	N/A	Yes	N/A	Brazil	Springer (1962)
macclurei	1		No	Yes	N/A	Yes	2	U. S. Atlantic and Gulf coasts and Caribbean	Re and Almeida (1981)
Parablennius		Unrestricted							
marmoreus	1		Yes	Yes	Yes	No	2	U. S. Atlantic and Gulf coasts south to Central America and Caribbean	Bath (1977, 1990*a*)
Scartella		Unrestricted							
cristata	0		No	Yes	No	No	6–16	Atlantic coast of Florida, Gulf, south to Central America	Bath (1970, 1977)

Gulf, Gulf of Mexico; N/A, information not available.

communities (*e.g.* barnacles and hydroids). Eggs are substratum-attached and deposited in clusters often inside bivalve shells. Several females may deposit eggs in the same nest, with each nest containing multiple cohorts at different stages of development. Males guard the nest until hatching, when larvae become planktonic (Labelle & Nursall, 1992).

Blenniids are territorial, demonstrate high site fidelity (Stephens *et al.*, 1970) and most species are widely distributed, abundant and easily collected. These life history traits make blennies potentially useful as 'environmental indicators' of habitat quality (Jacobsson *et al.*, 1986). Their crevicolous nature also contributes to successful invasion and colonization of new areas *via* ballast water transport (Wonham *et al.*, 2000). Despite the potential importance of blennies as 'environmental indicators' and their propensity to invade new areas *via* international shipping, the early life stages of only three of 20 WCNA blenniids have been adequately described: striped blenny *Chasmodes bosquianus* (Lacepede), Florida blenny *Chasmodes saburrae* Jordan & Gilbert and highfin blenny *Lupinoblennius nicholsi* (Tavolga). Early life stages of five additional blenniids were investigated in the present study.

MATERIALS AND METHODS

Presettlers (primarily postflexion stages) of five species of blenny were collected during light trap sampling from oil and gas platforms in the northern Gulf of Mexico off Louisiana from 1995 to 1997. These species included tessellated blenny *Hypsoblennius invemar* Smith-Vaniz & Acero, freckled blenny *Hypsoblennius ionthas* (Jordan & Evermann), featherduster blenny *Hypleurochilus multifilis* Bath, molly miller *Scartella cristata* (L.) and seaweed blenny *Parablennius marmoreus* (Poey), all in the sub-family Salariinae according to Bath (2001). *Hypsoblennius ionthas* is an estuarine and coastal species (Smith-Vaniz, 1980), *S. cristata* and *H. multifilis* are inner-shelf species often associated with rock jetties and petroleum platforms (Randall, 1966; Hastings, 1972), and *H. invemar* and *P. marmoreus* are mid-shelf species (Smith-Vaniz, 1980) often associated with petroleum platforms. A larva of the feather blenny *Hypsoblennius hentz* (Lesueur), presettlers of redlip blenny *Ophioblennius macclurei* (Silvester) and recent settlers of *C. saburrae* are illustrated for comparison with the species described here.

Recent settlers were hand-netted over oyster shell reefs and along rock jetties, collected with slurp guns along the legs of petroleum platforms, or following explosive removal of platforms. Specimens were fixed in 10% formalin and transferred to 70% ethanol after 24 h for long-term preservation. Specimens were dipped in a solution of cyanine blue 5R stain, also known as acid blue 113 (Saruwatari *et al.*, 1997), to improve anatomical contrast of sensory pores, fin rays and cephalic cirri. A developmental series of each of the five species was cleared and stained to reveal skeletal characters and observe general patterns of ossification following methods outlined in Potthoff (1984). Uptake of alizarin red differentiated calcification from alcian blue-stained chondrification. The process of calcification may begin before structures absorb alizarin red, but for practical purposes, stain uptake represents the onset of calcification (Dunn, 1983). Skeletal elements were considered formed when no blue remained, but does not imply that the process of calcification is complete.

The number and type of teeth change during development. Incisiform teeth have a flattened blade wider than the base and gradually replace the villiform teeth of early larvae. Teeth were counted along the left side of each jaw and the count doubled to determine the total number of teeth in each jaw. The symphysis of the premaxillae and of the dentary bones marked each jaw midline. Young of species with canines as adults have an elevated ridge of tissue along the gum line that conceals the developing canines. Mechanical abrasion of gums during specimen examination often exposes these 'precanines,' which gives the false impression that they have erupted. Canines are clearly recurved and longer than surrounding teeth. Pectoral rays are numbered in a dorsal to

ventral sequence to facilitate description of fin pigmentation patterns. Body lengths are reported as standard length (L_S) throughout, unless noted otherwise.

For descriptive purposes, each individual was assigned an interval of development following techniques described in Ditty *et al.* (2003). Labels assigned to intervals are 'larvae', 'metamorphs' and 'settlers' (Table II). The term larvae, as commonly understood in descriptive literature includes both the 'larvae' and 'metamorphs' categories used here. Voucher specimens are preserved in personal collections housed at NOAA Fisheries, Galveston Laboratory, TX, U.S.A.

MORPHOLOGICAL DEVELOPMENT

Two general pigmentation patterns are evident in the species described (Figs 1–5). The early life stages of all five species have a series of melanophores evenly spaced along the ventral midline of the tail that are closely associated with each anal fin pterygiophore. All five species also have pigment on the dorsum of the head and nape, over the dorsal surface of the visceral mass and on the medial side of the pectoral axil. Pigment ventrally along the visceral mass is sparse until late flexion.

'Larvae' of *H. invemar*, *H. ionthas*, *H. multifilis* and *S. cristata* have pigmentation pattern number 1, which is characterized by moderately-light to heavily-pigmented pectoral fins. Early postflexion larvae of most species also have pigment near the symphysis of the upper lip, on the lower jaw and cheek. Early 'metamorphs' have epidermal pigment dorsolaterally on the trunk just behind the nape. Trunk pigmentation increases with L_S and consolidates into bands or blotches in late 'metamorphs'. Trunk pigment seldom extends laterally beyond about mid-body before settlement (Figs 1–4).

Parablennius marmoreus has pigmentation pattern number 2, which is characterized by lack of pectoral fin ray pigment until just before settlement and a series of pigments along

TABLE II. Intervals of development for five species of blenny from the western central North Atlantic area. Note expanded size range for each interval when comparable intervals of development are combined across species

| Taxa	Interval of development	Number of specimens examined	L_S range (mm)
Hypleurochilus multifilis	Larvae	9	5·3–11·0
	Metamorphs	19	11·5–13·8
	Settlers	14	11·8–18·3
Hypsoblennius invemar	Larvae	15	5·4–11·0
	Metamorphs	19	11·0–13·5
	Settlers	18	11·8–18·3
Hypsoblennius ionthas	Larvae	15	5·0–9·1
	Metamorphs	18	9·7–11·5
	Settlers	8	11·7–17·3
Parablennius marmoreus	Larvae	22	5·8–13·0
	Metamorphs	19	13·5–21·5
	Settlers	9	19·0–20·5
Scartella cristata	Larvae	7	5·8–9·5
	Metamorphs	6	10·2–11·0
	Settlers	17	11·0–18·0
All species combined	Larvae	42	5·0–13·0
	Metamorphs	82	9·7–21·5
	Settlers	64	11·0–20·5

L_S, standard length.
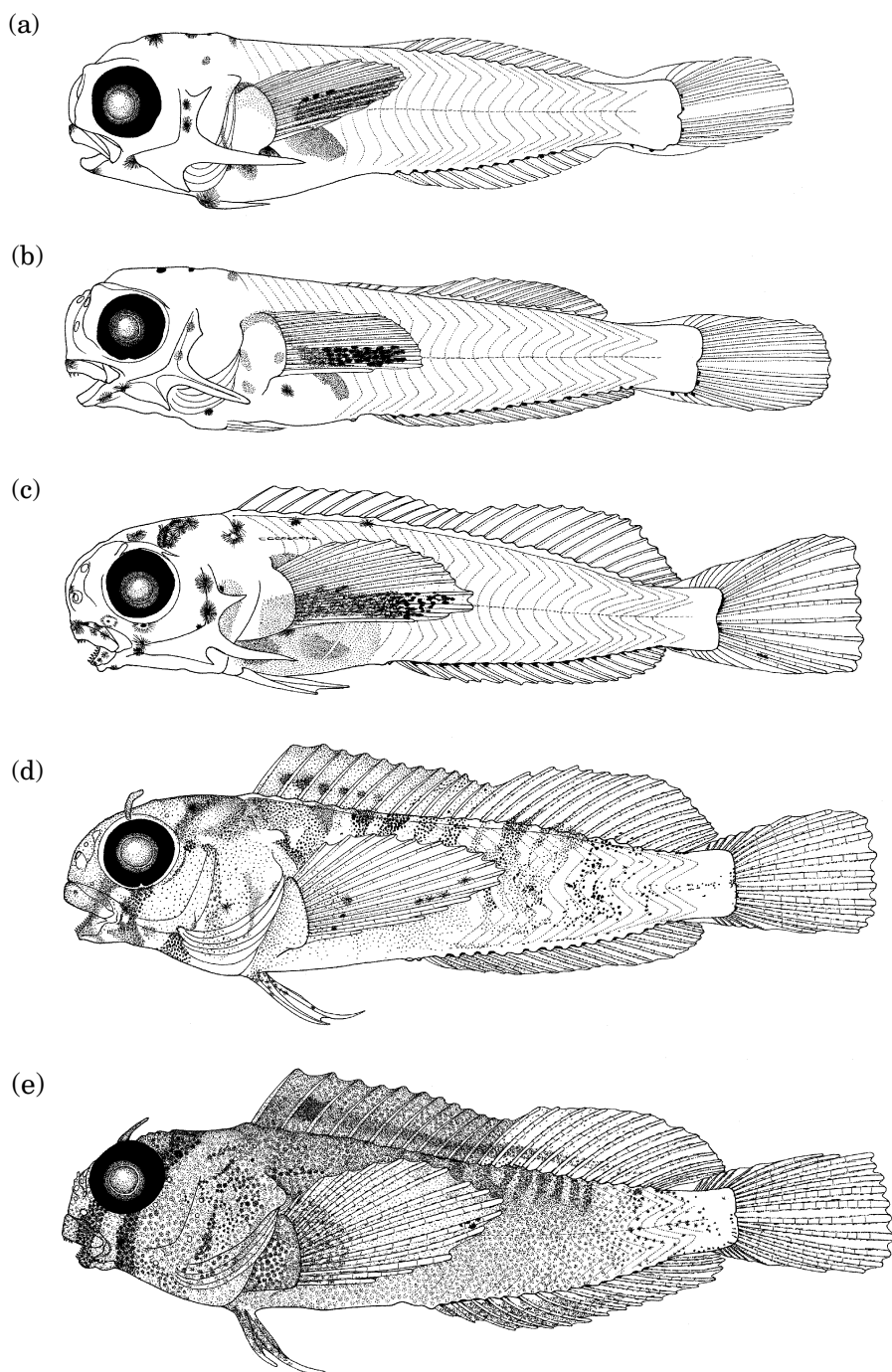
FIG. 1. Early life stages of *Hypsoblennius ionthas* from the western central North Atlantic. (a) 5·4, (b) 7·5, (c) 10·2, (d) 11·8 and (e) 12·7 mm L_S. (a), (b) 'larvae', (c) 'metamorph' and (d), (e) 'settlers'.
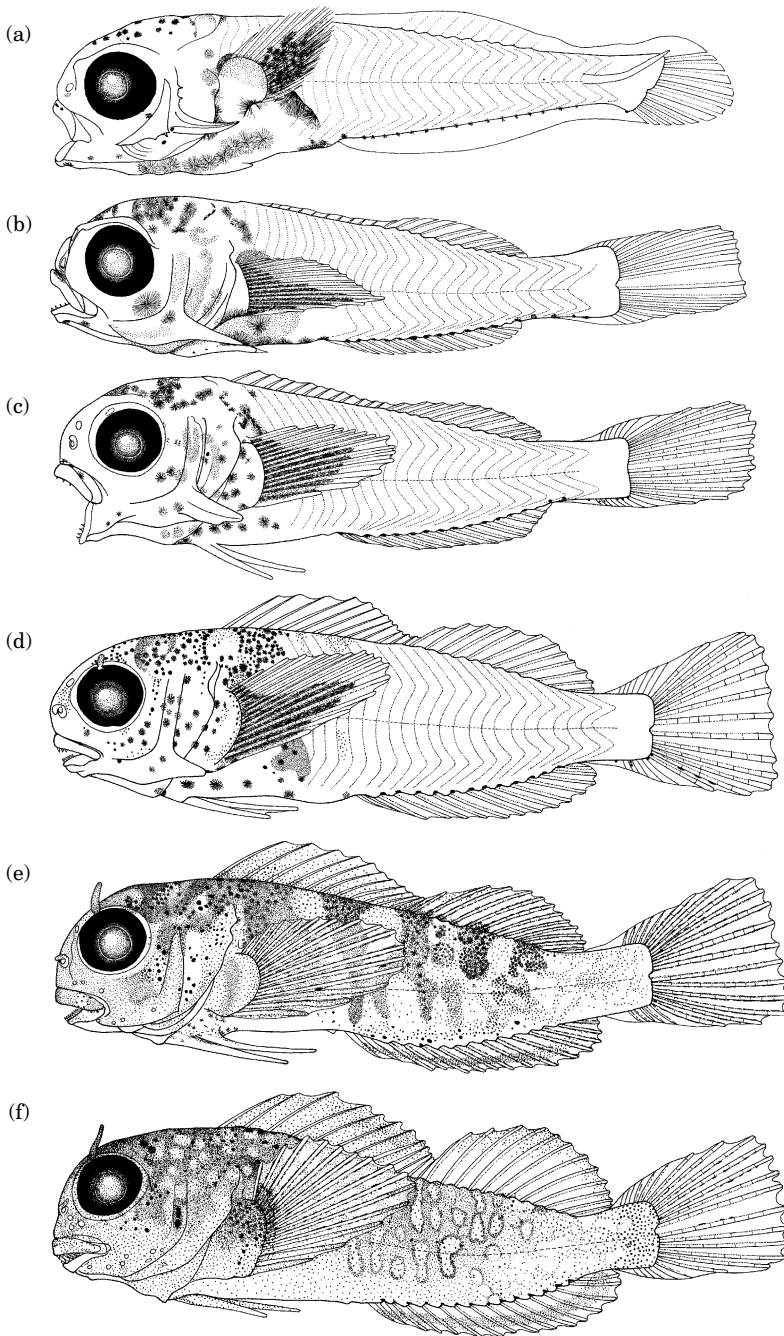
FIG. 2. Early life stages of *Hypsoblennius invemar* from the western central North Atlantic. (a) 5·1, (b) 7·0, (c) 10·4, (d) 12·7, (e) 13·0 and (f) 14·0 mm (L_S). (a), (b) 'larvae', (c), (d) 'metamorphs' and (e), (f) 'settlers'.
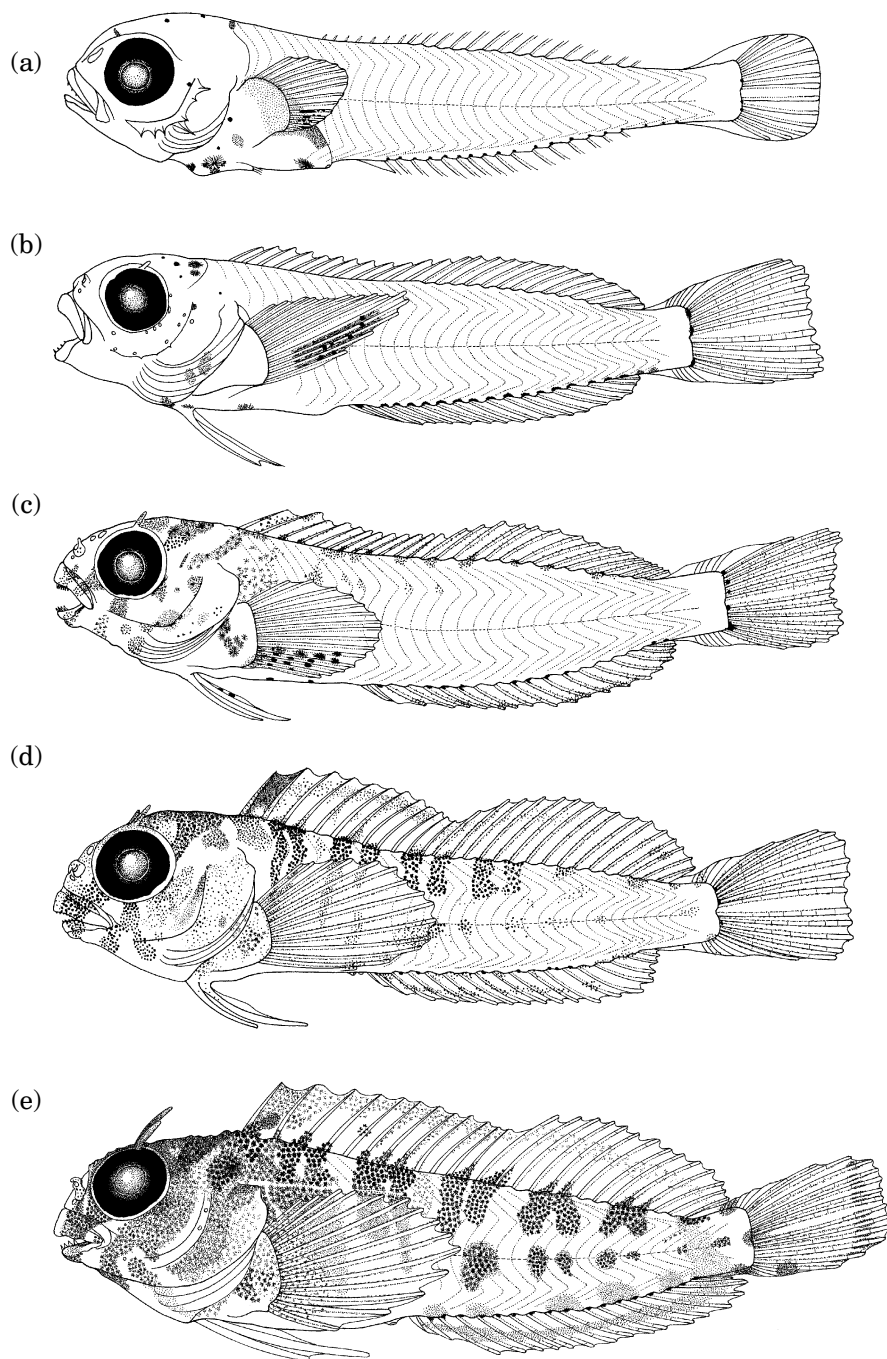
FIG. 3. Early life stages of *Hypleurochilus multifilis* from the western central North Atlantic. (a) 6·4, (b) 10·7, (c) 11·8, (d) 12·3 and (e) 14·5 mm (L_S). (a) 'larva', (b) early 'metamorph', (c) late 'metamorph' and (d), (e) 'settlers'.
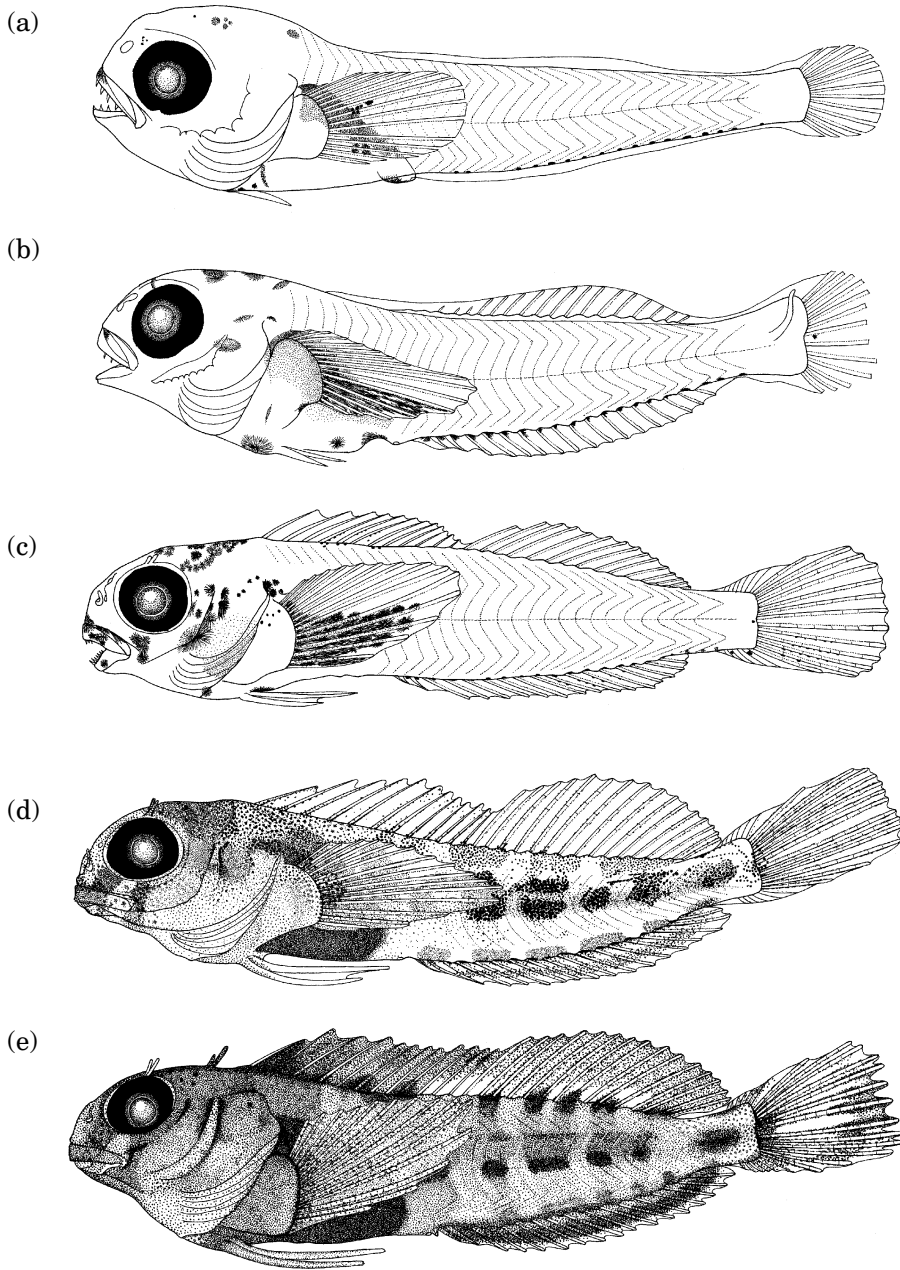
(a)

(b)

(c)

(d)

(e)

FIG. 4. Early life stages of *Scartella cristata* from the western central North Atlantic. (a) 5·3, (b) 7·3, (c) 10·2, (d) 12·0 and (e) 14·5 mm (L_S). (a), (b) 'larvae', (c) early 'metamorph' and (d), (e) 'settlers'.

the dorsal midline of the trunk in 'metamorphs'. 'Larvae' <9·0 mm have pigment on the medial side of the pectoral axil, but not on the fin rays. 'Larvae' have pigment along the outer margin of the preopercle by *c.* 9·0–10·0 mm, and near the symphysis of the upper lip by *c.* 12·0 mm. Ventrally, tail pigmentation resembles that of pattern number 1, except that *P. marmoreus* does not have pigment at the base of the first anal spine. Early
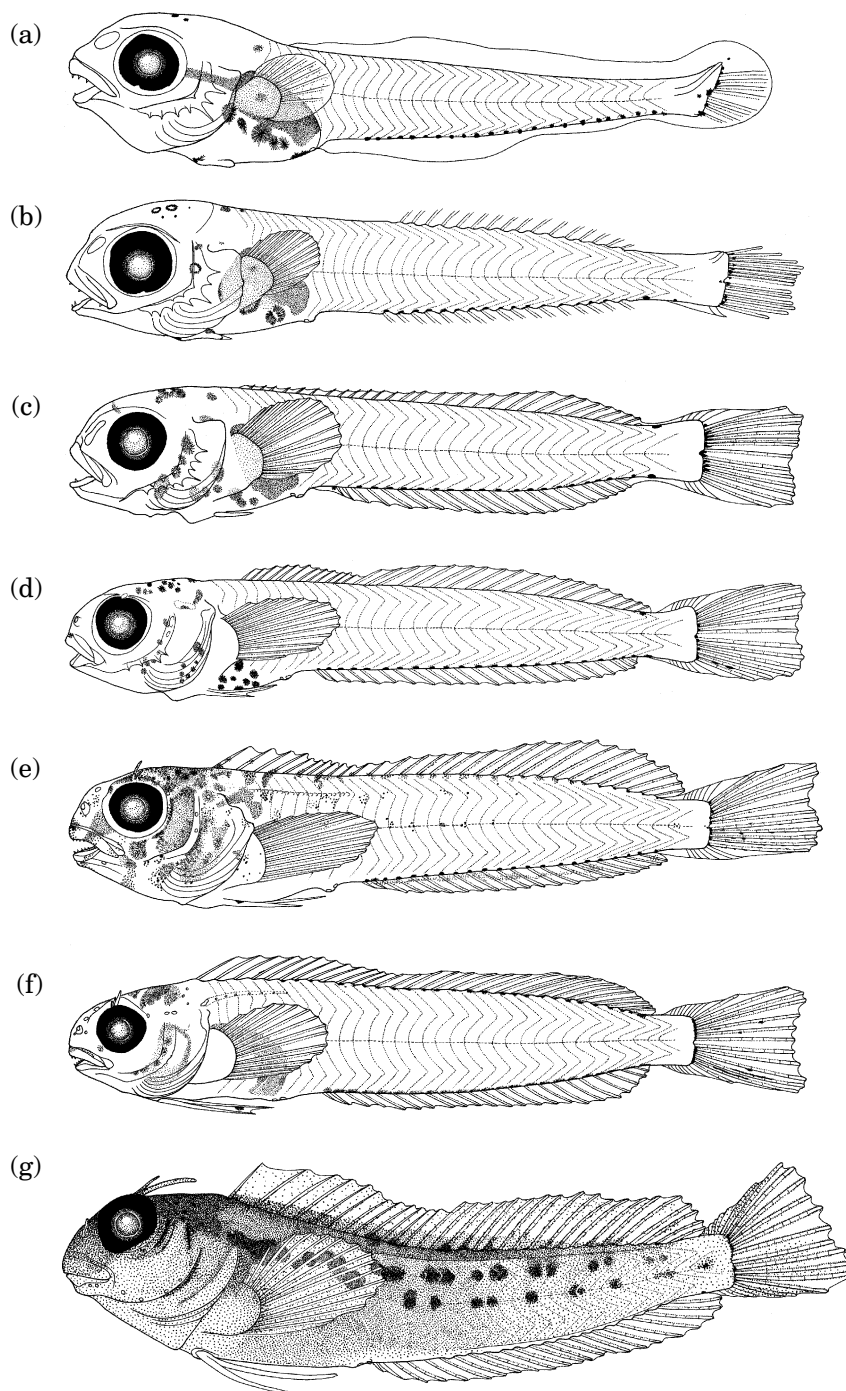
(a)

(b)

(c)

(d)

(e)

(f)

(g)

Fig. 5. Early life stages of *Parablennius marmoreus* from the western central North Atlantic. (a) 5·8, (b) 7·5, (c) 9·6, (d) 13·7, (e) 17·3, (f) 20·9 and (g). 23·0 mm (L_S). (a)–(c) 'larvae', (d) early 'metamorph', (e), (f) late 'metamorphs' and (g) 'settler'. Note intraspecific difference in size at given state of development for late 'metamorphs' (e), (f).

'metamorphs' have a single epidermal melanophore along the midline of the caudal peduncle behind the last dorsal pterygiophore by *c.* 13·5–14·0 mm. Late 'metamorphs' have a series of melanophores along the dorsal midline and pigment dorsolaterally along the trunk. The presence of a series of melanophores along the dorsal midline, proliferation of pigment over the head and trunk and pigment lightly scattered over the pectoral fin rays characterize *P. marmoreus* preparing to settle (Fig. 5).

Hypleurochilus multifilis and *S. cristata* have superficially similar pigmentation patterns and are difficult to separate. *Scartella cristata*, however, has pigment above the symphysis of the upper lip by 6·5 mm that *H. multifilis* lack until *c.* 12·0 mm (Figs 3–4). The number of epural bones and width of gill openings also differ between the two species (Table I). *Scartella cristata* has wide gill openings, with the lower margin of the operculum narrowly fused to the throat by a delicate branchiostegal membrane, so that a probe inserted under the outer margin of the operculum passes nearly unobstructed along the isthmus. *Hypleurochilus multifilis* has the operculum fused to the throat between the pectoral and pelvic fins. The delicate branchiostegal membrane is easily torn in 'larvae' and width of gill openings is difficult to determine until early transformation (*c.* 10 mm in these two species) when the membrane has thickened sufficiently to obstruct a probe.

The presence or absence and timing of pelvic fin pigmentation, and extent of pectoral fin pigmentation, is species-specific and helps separate some taxa (Table III). Late 'larvae' of *H. multifilis*, early 'metamorphs' of *P. marmoreus* and late 'metamorphs' of *S. cristata* have a melanophore on the longest pelvic fin ray, which *H. invemar* and *H. ionthas* lack until after settlement. Pectoral fin rays below the base of the 6th to the tip of the 14th ray are pigmented in presettlers of *H. ionthas*, whereas all rays below the 5th out to the 8th ray are pigmented in presettlers of *H. invemar* (Figs 1–2). All pectoral fin rays below the 9th or 10th (inclusive) and nearly 50% of the medial side of the axil are pigmented in presettlers of *H. multifilis* (Fig. 3). By *c.* 6·5 mm *S. cristata* have all pectoral rays below the base of the 6th out to the tip of the 15th ray pigmented (Fig. 4). At settlement, *c.* 35 to 50% of the original pectoral fin pigment remains in *H. invemar* and *H. ionthas*, whereas only scattered remnants of fin pigment remain in recent settlers of *H. multifilis* and *S. cristata*. *Parablennius marmoreus* lacks pectoral fin pigment until just before settlement (Fig. 5).

Formation and pigmentation of the orbital cirrus precedes that of the nasal cirrus in all species. The orbital cirrus initially forms as a thickening above the eye in late 'larvae' or early 'metamorphs'. The nasal cirrus develops about mid-way through metamorphosis in *H. invemar* [Fig. 2(d)], *H. multifilis* [Fig. 3(c)] and *S. cristata* [Fig. 4(c)], but not until just before settlement in *H. ionthas* [Fig. 1(e)] and *P. marmoreus* [Fig. 5(g)]. Whereas *H. invemar, H. multifilis* and *S. cristata* have lightly pigmented orbital and nasal cirri before settlement, the nasal cirrus remains unpigmented until after settlement in *H. ionthas* and *P. marmoreus*. Only *S. cristata* has nuchal cirri [Fig. 4(e)]. A settled 13·5 mm *S. cristata* had one nuchal cirrus, a 14·5 and 15·5 mm *S. cristata* (sex unknown) had two nuchal cirri and a 22·0 mm female had six nuchal cirri.

Length of the longest preopercular spine is species-specific, as is timing of spine resorption. Both species of *Hypsoblennius* have a prominent, elongate spine near the angle of the preopercle (Figs 1 and 2), whereas *H. multifilis* [Fig. 3(a)], *S. cristata* [Fig. 4(a)] and *P. marmoreus* [Fig. 5(a)–(d)] have a series of short preopercular spines along the outer shelf. Early 'larvae' of *P. marmoreus* also have one to three blunt spines along the inner shelf [Fig. 5(a), (b)]. All preopercular spines are resorbed in early 'metamorphs' of *H. multifilis, S. cristata* and *P. marmoreus* (Table III and Figs 3–5). *Hypsoblennius invemar* has a single elongate preopercular spine along the outer shelf [Fig. 2(a)–(d)], whereas *H. ionthas* has three prominent preopercular spines [the upper and lower spine of moderate length and an elongate middle spine; Fig. 1(a)–(c)]. The longest preopercular spine is not completely resorbed until after settlement in the two species of *Hypsoblennius* studied. Preopercular spine length easily separates presettlers of *Hypsoblennius* from *H. multifilis, S. cristata* and *P. marmoreus*.

All five blenniids have similar numbers and types of teeth at comparable stages of development (Table IV). In general, 'larvae' have <12 teeth, 'metamorphs' have 12–16 teeth and late 'metamorphs' and recent 'settlers' have ≥18 teeth. 'Metamorphs' and 'settlers' of *H. ionthas*, however, generally have two fewer teeth than do the other four

TABLE III. Some characters that help distinguish presettlement blenniids >5·0mm L_S from the western central North Atlantic area

Species	Pectoral fin rays pigmented (base outward to tip)[1]	Melanophore series along dorsal midline in 'metamorphs'	Preopercular spination — Mixed (short to moderate, variable)	Preopercular spination — Mixed (prominent, longest at angle)	Number — Pelvic soft rays	Number — Segmented caudal rays (mode)
Chasmodes bosquianus[2]	N/A[3]	No	Yes		3	11–12
Chasmodes saburrae[2]	2nd to 8th	No	Yes		3	11–12
Hypleurochilus multifilis[2]	Below 9th or 10th	No	Yes		3	13
Hypsoblennius hentz[2]	1st to 8–9th	No		Yes	3	13
Hypsoblennius invemar[2]	5th to 8th	No		Yes	4	13
Hypsoblennius ionthas[2]	6th to 14th	No		Yes	3	13
Lupinoblennius nicholsi[2]	4th to 6th	No	Yes		3	13
Ophioblennius macclurei[4]	None	Yes	Yes		4	13
Parablennius marmoreus[4]	None	Yes[5]	Yes		3	13
Scartella cristata[2]	6th to 15th	No	Yes		3	13
Others:						
Omobranchus punctatus	Light[6]	No[6]	Yes[6]	Yes[6]	2	13
Entomacrodus nigricans[7]	Light[6,8]	No[6]			4	13

[1]Dorsal ray is counted as first and ventral ray as last.
[2]Pigmentation pattern number 1.
[3]N/A, not available. Pattern probably similar to *C. saburrae*.
[4]Pigmentation pattern number 2.
[5]In 'metamorphs' from *c.* 14·0 mm L_S.
[6]Probable characters based on described congeners.
[7]May have serrate supraorbital crest.
[8]Pigment outlines outer margin of fin only.

TABLE IV. Number of lower jaw teeth in some blenniids from the western central North Atlantic area during different intervals of development

Taxa (number of lower jaw teeth in adults)	Life stage	L_S range of specimens (mm)	Number examined	Mean number of teeth	Number of teeth ±95% CI	Range
Hypleurochilus multifilis	Larvae	5·3–11·0	6	6·8	5·4–8·2	5–9
(20–35)	Metamorphs	11·5–13·8	21	14·2	13·5–15·0	12–17
	Settler	11·8–18·3	12	19·8	18·2–21·3	17–25
Hypsoblennius invemar	Larvae	5·4–11·0	10	9·5	8·3–10·7	8–14
(24–42)	Metamorphs	11·0–13·5	19	14·1	13·4–14·7	12–18
	Settler	11·8–18·3	18	21·1	19·7–22·5	17–27
Hypsoblennius ionthas	Larvae	5·0–9·1	7	8·7	8·3–9·2	8–9
(18–34)	Metamorphs	9·7–11·5	18	12·8	12·2–13·5	10–14
	Settler	11·7–17·3	8	18·8	16·0–21·5	16–25
Parablennius marmoreus	Larvae	5·8–13·0	14	9·1	8·4–9·9	8–12
(unknown)	Metamorphs	13·5–21·5	19	15·6	14·8–16·7	12–20
	Settler	19·0–20·5	8	20·5	19·9–20·6	20–22
Scartella cristata	Larvae	5·8–9·5	5	7·6	4·5–10·7	6–12
(20–34)	Metamorphs	10·2–11·0	6	15·5	14·6–16·4	14–16
	Settler	11·0–18·0	17	20·8	19·5–22·2	16–27

L_S, standard length.

species at comparable stages of development (Table IV). Villiform teeth first appear near the front corners of the upper and lower jaws before notochord flexion. Incisiform teeth form after flexion and protrude through foramina along the jaws. 'Transitional' spade-shaped teeth replace most villiform teeth in early 'metamorphs'; 'typical' incisiform-shaped teeth replace most transitional teeth just before settlement. Only *H. multifilis* and *P. marmoreus* have canine teeth. The canine teeth appear laterally behind the posterior-most incisors of each jaw in early 'metamorphs' of *P. marmoreus* (*i.e.* 14·0 mm L_S), but typically do not exceed the height of surrounding teeth until just before, and sometimes immediately after settlement. Canines erupt after settlement in *H. multifilis* and exceed the height of surrounding incisoriform teeth at *c.* 16·0 mm L_S.

The sequence of pore formation along the cephalic and lateral lines is similar in all species. Epidermis obscures cephalic pore openings in early 'larvae.' As the cephalic canals ossify and pore openings enlarge, cyanine blue stain penetrates and highlights the canal system. Pores are first visible along the lower jaw and operculum, followed by those along the otic, supratemporal and circumorbital canals. Lateral line pores and bony ossicles form in an anterior to posterior direction. Bony ossicles extend posteriad along the lateral line to below the 6th dorsal spine in late 'metamorphs' and along the entire upper portion of the lateral line prior to settlement.

Size at settlement is somewhat species-specific, but occurs within a narrow size window of *c.* 1·5 mm L_S in all species. *Hypsoblennius invemar*, *H. ionthas*, *H. multifilis* and *S. cristata* settle at mean sizes between 11·3 and 12·1 mm L_S, whereas *P. marmoreus* settles at a mean size of 19·3 mm L_S.

FIN DEVELOPMENT AND SKELETAL OSSIFICATION

All five blenny species have a similar sequence of fin formation (pectorals, primary caudal rays, dorsal and anal rays, pelvics, dorsal and anal spines, and secondary caudal rays). Incipient rays of the pectoral and caudal fins begin to form before notochord

flexion and segment during flexion. Dorsal and anal fin anlage appear shortly after flexion, followed by pelvic fin buds. Dorsal and anal rays form anteroposteriorly from mid-fin, with the terminal ray of each fin the last element to develop. Late 'metamorphs' of each species have all dorsal and anal fin rays initially segmented. Shortly after settlement, live or freshly-preserved specimens of each species have a stripe of iridescent chromatophores along the outer margin of the dorsal and anal fins. The primary caudal fin rays begin to bifurcate between 17 and 18 mm L_S in all species, except *P. marmoreus*. Caudal ray bifurcation is estimated to occur at 31·2 mm in *P. marmoreus*.

The primary hypural elements of the caudal complex and structures required for feeding and respiration develop first. The upper and lower jaws, branchiostegal rays, vertebral centra and primary hypural elements chondrify before notochord flexion and begin to ossify during flexion. Pectoral radials, neural and haemal spines, and dorsal and anal fin pterygiophores differentiate and chondrify during notochord flexion, and begin to ossify in late 'larvae' to early 'metamorphs,' but ossification of these structures remains incomplete until after settlement. Branchiostegal rays, pleural ribs and vertebral centra are ossified, for the most part, in early 'metamorphs.' The epurals, hypural 5 (when present), dentary and fourth and fifth infraorbitals are the last elements examined to ossify (in late 'metamorphs'), and remain incompletely ossified until after settlement.

SEXUAL DIMORPHISM AND TIMING OF SEXUAL MATURITY

Sexual dimorphism becomes increasingly evident after settlement (Table V). Shortly after settlement, females of *H. ionthas* have a pigmentation pattern that resembles 'freckles' along the lower part of the head. Males of *H. ionthas* lack 'freckles' and also have longer orbital cirri than females. Generally, sexually dimorphic differences are evident by 14–15 mm (consistently so by 17–18 mm), except in *P. marmoreus*, which apparently mature at a larger size because no *P. marmoreus* captured exhibited evidence externally of being in spawning condition. The two smallest blennies captured with the external characters normally associated with being sexually mature were a 20 mm male and 21 mm female *H. multifilis*. Primary caudal fin rays begin to bifurcate between 17·0 and 18·3 mm in *H. invemar, H. ionthas, H. multifilis* and *S. cristata*. *Hypleurochilus multifilis* display the external characteristics of being sexually mature at 20–21 mm. Thus, bifurcation of primary caudal fin rays is an indicator of approaching sexual maturity in *H. multifilis* and this may also be true in the other species studied here.

DISCUSSION

Estuarine and coastal blennies, including *H. ionthas*, *H. hentz* [Fig. 6(a)], *C. saburrae* [Fig. 6(b)–(d)], *C. bosquianus*, and the two species of *Lupinoblennius* share pigmentation pattern number 1 with *H. multifilis* and *S. cristata*. Presettlers with pattern number 1 are characterized by moderately-light to heavily-pigmented pectoral fins (Table III). In addition, 'metamorphs' with pattern number 1 lack the series of melanophores along the dorsal midline between the nape and caudal peduncle. Reduction in pectoral fin pigment and development of a mottled pigmentation pattern along the trunk just before settlement may help conceal new demersal recruits from visual predators during the settlement process (Moser, 1981). Presettlers of *P. marmoreus* (Fig. 5) and *O. macclurei* [Fig. 6(e), (f)] share pigmentation pattern number 2 characterized by a melanophore dorsally on the caudal peduncle in 'larvae' and later a series of melanophores along the dorsal midline in 'metamorphs', and no pectoral fin pigment, except medially behind the pectoral axil, until just before settlement. The fact that presettlers of *P. marmoreus* and *O. macclurei* occupy offshore

TABLE V. Sexual dimorphism in some blenniids from the western central North Atlantic area. Blenniids nearing maturity can be sexed by differences in anal fin ray shape. The urogenital opening also forms a papilla in males and is concealed by a hood of tissue in females, although this character is difficult to verify at sizes <15 mm standard length (L_S). No published information is available for *Hypleurochilus multifilis* and *Parablennius marmoreus*

Taxa	Sexual dimorphism		References
	Males[1]	Females[2]	
Chasmodes bosquianus[3]	Longer maxillary		Springer (1959); Smith (1974); Williams (1983)
Hypsoblennius hentz	Longer, broader supraorbital cirrus		Smith-Vaniz (1980)
Hypsoblennius invemar[4]	Longer, broader supraorbital cirrus		Smith-Vaniz (1980)
Hypsoblennius ionthas[4]	Longer, broader supraorbital cirrus		Smith-Vaniz (1980)
	Weakly or not freckled	'Freckled' on lower 50% of face	
Lupinoblennius nicholsi	Elongate first dorsal spine	Longer snout than males at >20 mm L_S	Tavolga (1954)
	Thickened, fleshy first dorsal ray		
	Upper and lower canines at maturity	Lower canines only	
Lupinoblennius vinctus	Longer, broader supraorbital cirrus		Dawson (1970)
	Basal notch anterior to 1st dorsal fin	No basal notch	
	Upper and lower canines	Lower canines only	
Ophioblennius macclurei[3]			Springer (1962); Smith (1974)
Scartella cristata[3,4]	First anal spine obvious	First anal spine small, barely visible	Smith (1974)

[1]First-two anal spines with flattened, spatulate pads that often become fleshy, rugose, glandular knobs during the breeding season.
[2]First anal spine often embedded in the urogenital aperture.
[3]Breeding males have fleshy lateral extensions at the tips of the anal fin rays and bear spatulate pads on the first-two anal spines.
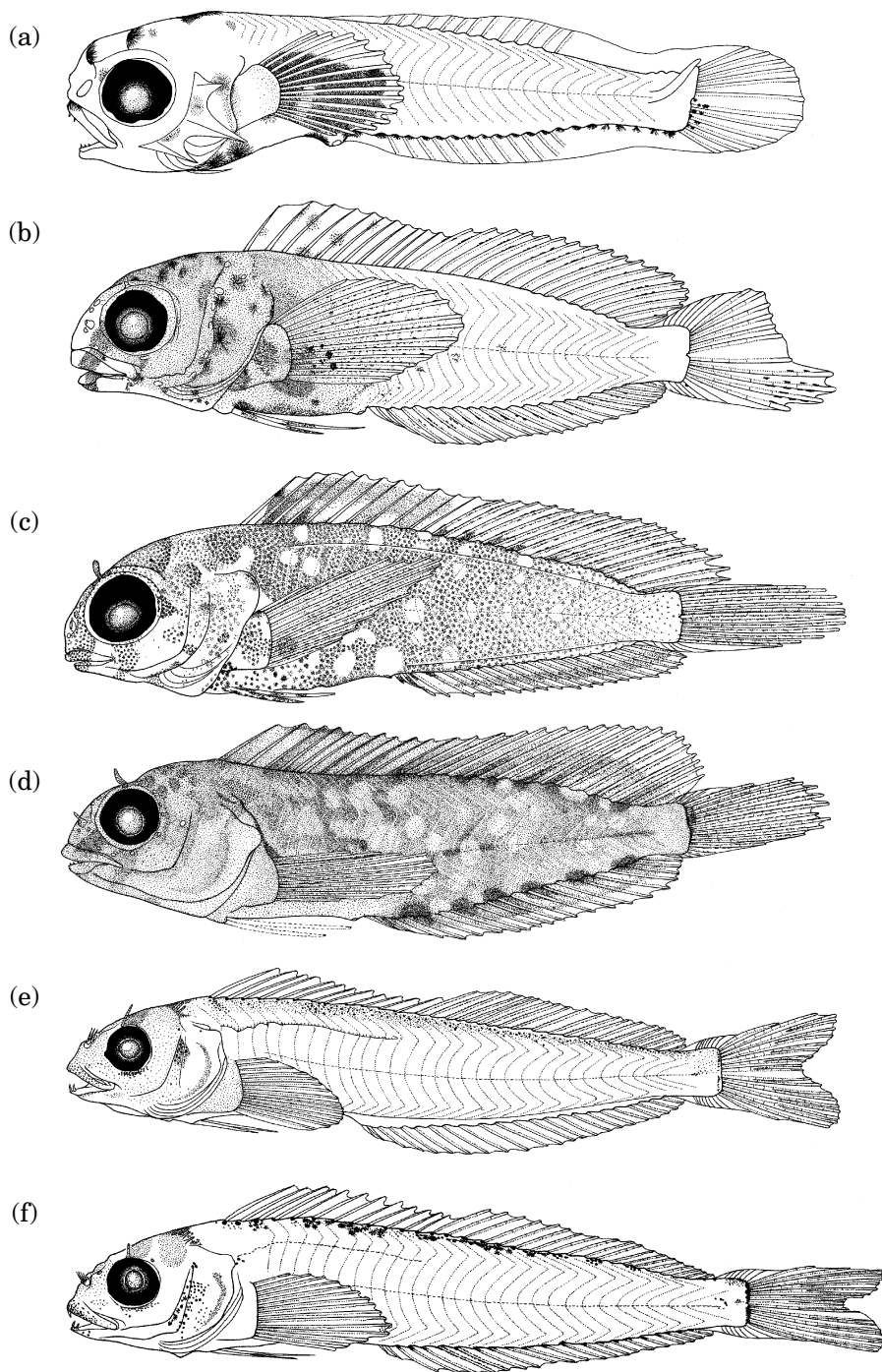[4]One of the five species studied.

(a)

(b)

(c)

(d)

(e)

(f)

FIG. 6. Early life stages of other species of blenny from the western central North Atlantic. (a) 'larva' of *Hypsoblennius hentz*, 5·0 mm L_S. (b) 8·5, (c) 11·0 and (d) 18·0 mm L_S 'settlers' of *Chasmodes saburrae*. (e) 38·0 and (f) 46·0 mm L_S late 'metamorphs' of *Ophioblennius macclurei*. Note intraspecific difference in size at given state of development for late 'metamorphs' (e), (f).

waters and differ in pigmentation pattern from the coastal and estuarine species suggest that interspecific differences in pigmentation may reflect adaptive convergence to similar ecological niches (Bryan & Madraisau, 1977; Kendall, 1991). Pelagic young of species with heavily-pigmented pectoral fins would be at a disadvantage in less turbid offshore waters because dark pectoral pigment against a light background could be an important clue to visual predators. The fact that *H. ionthas* (Table IV) and two other primarily estuarine genera, *Chasmodes* and *Lupinoblennius*, have fewer teeth (Peters, 1981, 1985) at comparable stages of development than species residing primarily over the mid- and outer-continental shelf is consistent with an ecological relationship among some taxa.

Accurate discrimination of young *H. ionthas* (Fig. 1) from *H. hentz* [Fig. 6(a)] remains problematic in areas of overlap because both species have three prominent preopercular spines and a similar pigmentation pattern. By late postflexion, however, differences in pectoral fin pigmentation and the number of pores along the mandible separate the two species. Pectoral fin rays from the base of the 6th to the tip of the 14th ray are pigmented in *H. ionthas*, whereas the 1st ray out to the tip of the 8th or 9th ray are pigmented in *H. hentz* (Table III). In addition, *H. ionthas* has three mandibular pores and *H. hentz* has four pores, although pores are difficult to detect until the lower jaw ossifies and openings enlarge. Differences between *H. ionthas* and *H. hentz* in shape of the fleshy flap of the lower lip (Smith-Vaniz, 1980) are insufficient to separate the two species until late metamorphosis or after settlement.

Patterns of structural development are consistent with the ecological necessities of feeding and swimming, as has been suggested for other fishes (Dunn, 1983; Osse *et al.*, 1997; Gisbert, 1999; Wagemans & Vandewalle, 2001). Rapid ossification of the epural bones and other caudal elements just before settlement may improve caudal dexterity and predator avoidance during and after settlement. Similarly, completion of infraorbital bone ossification after settlement permits eye reorientation during metamorphosis to the final position in demersal adults (Gatz, 1979; Watson, 1987).

Blenniid larvae are difficult to identify to species for several reasons: meristic characters often overlap and counts are incomplete for many species, adult characters are not developed (Cavalluzzi, 1992) and some species require clearing and staining to obtain the structural characters necessary for species separation. Differences in the following characters are diagnostic for some genera and species (Tables I and III): number of dorsal, anal, pelvic and caudal fin elements, number of mandibular pores, pectoral fin pigmentation pattern, presence or absence of canine teeth and hypural 5, and width of gill openings. Whether canine teeth and hypural 5 are present, however, cannot be ascertained until just before and sometimes after settlement when these structures are adequately developed. Similarly, width of the gill openings is difficult to determine until the branchiostegal membrane has thickened sufficiently to obstruct a probe passed along the outer margin of the operculum.

Incorrect species identification and unrecognized and cryptic species will create problems in determining species distributions. For example, only *Hypleurochilus geminatus* (Wood) was thought to occur along the Atlantic and Gulf coasts of the U.S. for many years. Bath (1994), however, revised the genus and found four species of *Hypleurochilus* in U. S. Atlantic and Gulf coast

TABLE VI. Synopsis of some characters that separate blennioid families from the western central North Atlantic area. Larval characters are compiled from information available for species with described early life stages. Consequently, there may be exceptions to the characters listed for a given family. Data compiled primarily from Cavalluzzi (1992), Springer (1993), Watson (1996) and Neira *et al.* (1998). Clinids are unknown from the region

Characters	Family				
	Blenniidae	Chaenopsidae	Dactyscolopidae	Labrisomidae	Tripterygiidae
Adults					
Dorsal fin divided	Continuous [1]	Continuous [1]	Continuous [1]	Continuous [1]	Yes [2]
Dorsal fin spines	<14	>16	7–17	>16	III + X–XIII
Dorsal fin rays	12–22	Rarely >21 [3]	12–32	Rarely >12 [4]	Rarely >12
Total anal fin elements	<23 [5,6]	20–39	23 or more [5]	16–31	16–19
Segmented caudal fin rays	12–14 [6]	12–14	10–11 (rarely 12)	12–14	15
Number of vertebrae/myomeres	30–36 [6]	>39	>35	32–39	30–35
Branched dorsal/pectoral/caudal fin rays	No/No/Yes	No/No/No	No/No/Some	No/No/Some	Some/Some/Yes
Gill membranes separate and free from isthmus	No	No	Yes	No	No
Margin of interopercle and opercle scalloped	No	No	Yes	No	No
Lateral line present (length varies)	Yes	Rarely with	Yes	Rarely without	Yes
Scales	No	Rarely with	Yes	Rarely without	Yes
Premaxillae protractile	No	Yes	Yes	Yes	Yes
Lower jaw longer than upper jaw	No [7]	No	No	No	No
Teeth (conical; biserial in some part of jaw)	Some [6]	Yes	Yes	Yes	Yes
Canine teeth	Rarely	No	No	No	No
Free margin of lips fimbriate or lappeted	Rarely [6]	No	Yes	No	No [8]
Nuchal cirri	Rarely [6]	No	No	Most	No
Hypural 5	Some [6]	Some	No	Some	Rarely without
Larvae and presettlement 'metamorphs'					
Length of opercular spines	Variable	Short, if any	Short, if any	Mostly short; few, if any	Short, if any
Pectoral fin pigmentation (presettlement)	Heavy in most	None	None	None	None
Epidermal pigment on dorsum of head	Multiple	None to few	Rarely at <9–10 mm	None to few	One to few
Pigment internally on parasphenoid (below orbit)	Some	No	Yes	No	No
Pigment along dorsal midline of caudal peduncle	Rarely	Some	Rare, if present	Some	Common
Pigment ventrally along tail regularly-spaced	Yes	Yes	Yes	Irregular to regular [9]	Yes

Pigment dorsally over visceral mass conspicuous	Yes	Yes	None to small patch	Yes	No
Swimbladder conspicuous; dorsal surface pigmented	No [10]	Yes	Yes; small patch	Yes	Yes
Pigment ventrally behind pelvic fin insertion	Common	Rarely [10]	2 to 4	Rarely [11]	Rarely [11]
Pigment dorsally on hindgut near anus	Rarely [12]	Common	No	Common	Light, if any
Pigment ventrally on hindgut near anus	Common early	Common early	Rarely, if present	Common early	Rarely, if present
Preanal length	35–50%	40–45%	35–40%	45–55% (>50%)	40–50%

[1]Dorsal fin usually continuous but membrane between spines and soft-rays may be deeply incised.
[2]Separation between first spinous and second spinous dorsal fins complete; gap always present.
[3]Only one (*Chaenopsis*) of nine genera with >25 dorsal rays.
[4]Occasionally dorsal fin without spines.
[5]Species of dactyscolopids that overlap blenniids with 23 to 26 total anal fin elements only have three spines in first dorsal fin.
[6]See Table 1 for exceptions.
[7]Teeth incisiform and uniserial.
[8]Except for one Indo-Pacific species, *Helcogramma rhinoceros*.
[9]Pigments irregularly-spaced early, but ventral series usually becomes regularly-spaced after notochord flexion.
[10]Swimbladder usually invisible externally.
[11]If present, pigment placed immediately behind pelvic fin base only.
[12]In postflexion larvae.

waters. Of the four species, only *H. geminatus* occurs in the Chesapeake Bay region where Hildebrand & Cable (1938) obtained larvae they describe as *H. geminatus*. Hildebrand & Cable (1938) mixed illustrations of *C. bosquianus* larvae with their description of *H. hentz*, an error that has been perpetuated by many authors. In fact, only the 12·0 mm total length, L_T, specimen in Hildebrand & Cable (1938) is *H. hentz*. The 2·6 mm larvae cannot be positively identified at this time, but the 3·0, 4·45 and 6·2 mm L_T specimens illustrated as *H. hentz* are *C. bosquianus*. The identity of preflexion larvae described by De Leo *et al.* (1976) as *S. cristata* is problematic, although *S. cristata* is found in the Mediterranean Sea along the Italian coast (Bath, 1990*b*; Nieder *et al.*, 2000).

The Blenniidae includes four sub-families (formerly tribes; Bath, 2001) of which two, Omobranchinae and Salariinae, occur in the WCNA area. The Parablenniini is a junior synonym of Salariini and both former tribes have been united in the sub-family Salariinae (Bath, 2001). Some salariins (only *Ophioblennius* and *Entomacrodus* from the WCNA area) have a specialized pelagic stage known as the 'ophioblennius'. The 'ophioblennius' is characterized by retaining the canine-like teeth near the anterior corners of the lower or both jaws, elongate pectoral fins and pigmentation pattern of larvae, while possessing the large body size and cirri development typical of early juveniles [Fig. 6(e), (f); Springer, 1967; Labelle & Nursall, 1985; Watson, 1996]. Based primarily on descriptions of conspecifics from other areas, early life stages of regional *Ophioblennius* and *Entomacrodus* would be expected to have relatively small preopercular spines of mixed length that are resorbed early in development, and elongate, unpigmented or lightly-pigmented pectoral fin rays (Table III). *Entomacrodus* larvae would also be expected to have a series of supraocular spines. A 5·0 mm *Ophioblennius* larva, the largest 'non-ophioblennius' stage illustrated by Labelle & Nursall (1985), has eight preopercular spines of mixed length and a melanophore dorsally on the caudal peduncle near the termination of the dorsal fin. Recent genetic evidence suggests that the *Ophioblennius atlanticus* (Valenciennes) complex in the eastern and western Atlantic may include five distinct geographic lineages (Muss *et al.*, 2001).

Uniting Parablenniini and Salariini into Salariinae (Bath, 2001) requires re-evaluation of larval characters generally considered diagnostic of salariins. For example, not all salariin larvae have pectoral fin pigment (*i.e. P. marmoreus* and *O. macclurei*) before late transformation. Whether larvae of all WCNA salariins have a series of melanophores along the ventral midline of the tail associated with anal-fin pterygiophores is unclear. Labelle & Nursall (1985) do not discuss this ventral midline series of pigments in *Ophioblennius*, but the 5·9 mm L_T larva they illustrate has this ventral series. Early life stages of eastern Pacific *Ophioblennius steindachneri* Jordan & Evermann and *Entomacrodus chiostictus* (Jordan & Gilbert) (Watson, 1996) lack pigment on the anal-fin pterygiophores. Other characters (*e.g.* head and gut shape and length of preopercular spines) also vary widely within the subfamily, but should help define the four species-groups recognized by Bath (2001).

Omobranchus punctatus (Valenciennes), the only regional omobranchin, has fewer pelvic rays and higher vertebral, dorsal and anal fin counts than other blenniids, except *O. macclurei* (Table I). Described larvae of *Omobranchus* from other areas (Watson, 1996; Neira *et al.*, 1998) suggest that pelagic *O. punctatus*

will have a broad, elongate spine near the angle of the preopercle and sparse pectoral fin pigment. The posterior pair of lower canines in omobranchins usually develop during flexion or early postflexion and are typically smaller than the prominent anterior canines found in some salariins of comparable stage (Watson, 2000). All omobranchins, except an Indian Ocean species, *Laiphognathus multimaculatus* Smith, lack cephalic cirri.

Other blennioid families in the WCNA are: Chaenopsidae, Dactyloscopidae, Labrisomidae and Tripterygiidae (Springer, 1993). A sixth family, Clinidae, is unknown from the area (Cavalluzzi, 1992). Taxonomic membership in the Labrisomidae is uncertain and monophyly remains to be hypothesized cladistically (Springer, 1993). While traits that characterize families are known (Table VI), early life stages are difficult to separate because many anatomical characters remain poorly developed until late transformation. In general, blennioid larvae have a relatively short gut (35 to 50% L_S). Preopercular spines are often short (if present), but can be elongate in some blenniids, especially *Hypsoblennius*. Once formed, the dorsal fin is long-based and continuous (but may be deeply-divided), except in

TABLE VII. Blennioids from the western central North Atlantic area with described early life stages

Taxa	'Larvae'	'Metamorphs'	'Settlers'	Literature
	Stage		
Family Blenniidae				
Chasmodes bosquianus[1]	X	X		Hildebrand & Cable (1938)
Chasmodes saburrae	X	X	X	Peters (1981); this study
Hypleurochilus geminatus	X	X		Hildebrand & Cable (1938)
Hypleurochilus multifilis	X	X	X	This study
Hypsoblennius hentz[1]	X	X		Hildebrand & Cable (1938); This study
Hypsoblennius invemar	X	X	X	This study
Hypsoblennius ionthas	X	X	X	This study
Lupinoblennius nicholsi	X	X	X	Peters (1985)
Ophioblennius macclurei	X	X		Labelle & Nursall (1985); This study
Parablennius marmoreus	X	X	X	This study
Scartella cristata	X	X	X	This study
Family Chaenopsidae				
Several morphotypes	X			Cavalluzzi (1992)
Family Dactyscolopidae				
Gillellus jacksoni	X			Cavalluzzi (1992)
Gillellus uranidea	X			Cavalluzzi (1992)
Family Labrisomidae				
Paraclinus sp.	X			Cavalluzzi (1992)
Labrisomus/Malacoctenus sp.	X			Cavalluzzi (1992)
Stathmonotus hemphilli	X			Cavalluzzi (1992)
Stathmonotus stahli	X			Cavalluzzi (1992)
Family Tripterygiidae				
Enneanectes sp. morph 1	X			Cavalluzzi (1992)
Enneanectes sp. morph 2	X			Cavalluzzi (1992)
Enneanectes sp. morph 3	X			Cavalluzzi (1992)

[1]Illustrations and description in Hildebrand and Cable (1938) are a mixture of these two species.

tripterygiids, which have the spinous dorsal fins separated by a gap. The pectoral fins are unpigmented in blennioids, except in blenniids, which have moderately-light to heavily-pigmented pectoral fins in all but a few taxa. Blennioid larvae commonly have pigment over the visceral mass and along the ventral midline of the tail, but pigment dorsally and laterally on the trunk is uncommon before metamorphosis, except in tripterygiids. Most blennioid families also have a conspicuous, externally visible swimbladder (Table VI). Cavalluzzi (1992) indicates that most blenniid larvae have pigment on the roof of the mouth. If so, this may be a potentially useful character for separating blenniid larvae from those of other blennioid families. Larvae of the five salariins described here, however, do not have such pigment.

The present understanding of the larval characters that unite or distinguish blennioid families and sub-families is incomplete. In fact, other than for blenniids, descriptions of early life stages are limited primarily to morphotypes (Table VII). As a result, the utility of larval characters in better understanding blennioid phylogeny must await the description of early life stages of other blennioid families.

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